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RESEARCH PAPER

Giant rodents from the Neotropics: diversity and dental variation of late Miocene neoepiblemid remains from Urumaco, Venezuela

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Abstract Caviomorphs constitute a large evolutionary radiation of South America rodents, exhibiting a wide range of body size and ecomorphological disparity. The geological history of caviomorphs has been recorded mainly from high latitudes, besides isolated discoveries from the Neotropics. The late Miocene fauna from Urumaco, Venezuela, is noteworthy for its location and for preserving the giant rodent *Phoberomys pattersoni*. Previous studies of isolated postcranial remains suggested that the rodent diversity from Urumaco was higher than is currently recognized. Based on new remains we document dental variation that indicates the presence of at least two giant rodent taxa in Urumaco, including *Neoepiblema*. Quantitative analysis of dentition of the different neoepiblemid species supports the differentiation between *Neoepiblema* and *Phoberomys* and suggests that several recognized species of *Phoberomys* could represent different ontogenetic stages of one or few taxa within the genus.

Keywords Mammalia · Caviomorpha · South America · Neogene · Body size · Paleobiology

Kurzfassung Die Caviomorpha stellen eine grosse evolutionäre Radiation südamerikanischer Nagetiere dar. Die geologische Geschichte der Caviomorpha ist, neben isolierten Entdeckungen in der Neotropis, hauptsächlich von den hohen Breiten überliefert. Die spätmiozäne Fauna von Urumaco, Venezuela, ist bemerkenswert für ihre Lage und für die Erhaltung von *Phoberomys pattersoni*. Vorhergehende Studien isolierter postcranialer Überreste deuteten darauf hin, dass die Diversität der Riesennager von Urumaco größer war als gegenwärtig angenommen. Basierend auf neuen Überresten dokumentieren wir dentale Variation, die auf die Anwesenheit von mindestens zwei verschiedenen Riesennager-Taxa in Urumaco, einschliesslich *Neoepiblema*, hinweist. Eine quantitative Analyse des Gebisses der verschiedenen neoepiblemiden Arten unterstützt die Unterscheidung zwischen *Neoepiblema* und *Phoberomys*, und deutet darauf hin, daß verschiedene anerkannte Arten von *Phoberomys* unterschiedliche ontogenetische Stadien eines oder mehrerer Taxa innerhalb einer Gattung repräsentieren könnten.

Schlüsselwörter Mammalia · Caviomorpha · Südamerika · Neotropis · Neogen · Körpergröße · Paläobiologie

Abbreviations

AMU-CURS	Alcaldía del Municipio de Urumaco, Falcón, Venezuela
CIAAP-UNEM	Centro de Investigaciones Antropológicas Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela
MCNC	Museo Nacional de Ciencias, Caracas, Venezuela
MLP	Museo de La Plata, La Plata, Argentina
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
SALMA	South American land mammal age
M-m	Molar

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P-p	Premolar
AP	Anteroposterior length
AW	Anterior width
PW	Posterior width
MW	Medium width

Introduction

Caviomorphs constitute a large radiation of South America rodents, exhibiting a wide range of body size and morphological disparity, including terrestrial, fossorial, semiaquatic, scansorial and arboreal representatives (Mares and Ojeda 1982; Weisbecker and Schmid 2007). The group likely arrived from Africa by rafting, with the first appearance of a stem caviomorph recorded in the middle Eocene of the Peruvian Amazonia (Yahuarango Formation; 41.6–40.94 Ma; Antoine et al. 2012). The molecular evidence and fossil record support the appearance of main clades ('superfamilies/families') within Caviomorpha during the late Eocene to early Oligocene (Vucetich et al. 1999; Fabre et al. 2012; Voloch et al. 2013), whereas most of the living 'families' radiated between the middle and late Miocene (Vucetich et al. 1999; Opazo 2005; Pérez and Pol 2012; Upham and Patterson 2012).

The long history of caviomorphs has been recorded, as is the general case from South America, from high latitudes (e.g., Wood and Patterson 1959; Vucetich et al. 1993, 1999, 2010a, b, 2014; Kramarz and Bellosi 2005; Flynn et al. 2008; Rinderknecht and Blanco 2008; Nasif et al. 2013), but the northern Neotropics have also provided significant discoveries (MacFadden 2006). The tropical faunas of Santa Rosa (late Eocene; Campbell 2004) and Contamana (middle Eocene; Antoine et al. 2012) of Peru, La Venta in the middle Miocene (Laventan SALMA) of Colombia (Kay et al. 1997), Urumaco in the late Miocene of Venezuela (Sánchez-Villagra et al. 2010) and Acre (Solimões Formation) in the middle to late Miocene of Amazonia (Cozzuol 2006; Ribeiro et al. 2013) are noteworthy, because of the diversity they preserve. The new tropical fossil assemblages of Fitzcarrald in middle Miocene (Laventan) sediments of the Peruvian Amazonia (Tejada-Lara et al. 2015) and Castilletes middle Miocene-early Pliocene in northern Colombia (Moreno et al. 2015) add important data to the Neotropical fossil record. The Greater Antilles have also been a source of significant discoveries (MacPhee 2011; MacPhee and Flemming 2003). As in northern South America, the most remarkable aspect of some Caribbean rodents has been their very large size (Silva Taboada et al. 2007).

Among the caviomorphs the Neoepiblemidae, including *Neoepiblema*, *Eusigmomys* and *Phoberomys* (Negri and Ferigolo 1999), are among the largest ones. Phylogenetic analyses suggest a close relationship between *Phoberomys* and *Dinomys*, the pacarana, among extant taxa (Sánchez-Villagra et al. 2003; Horovitz et al. 2006), but the phylogenetic relationships of these and other extinct and large caviomorphs are in need of study (Kramarz et al. 2013). Phylogenetic analyses based on molecular data support the close affinities between Dinomyidae and Chinchillidae (Opazo 2005; Huchon et al. 2007; Blanga-Kanfi et al. 2009; Fabre et al. 2012; Upham and Patterson 2012).

Phoberomys pattersoni is the largest neoepiblemid and is known based on an almost completed skeleton from the late Miocene deposits of the Urumaco Formation (Mones 1980; Bondesio and Bocquentin-Villanueva 1988; Sánchez-Villagra et al. 2003; Horovitz et al. 2006). Body mass estimates resulted in extreme sizes ranging from 220 to 450 kg (Millien and Bovy 2010; Geiger et al. 2013). Previous studies suggested that giant rodent diversity from Urumaco was higher than is currently recognized, either based on a few craniodental remains (Horovitz et al. 2006, 2010) or on isolated femora that cannot be used for definitive taxonomic assignations (Geiger et al. 2013). The taxonomy of these rodents is based largely on dental features (Table 1). There are size and morphological intraspecific variations in euhypsodont teeth, which are important to consider in order to understand the taxonomy and ontogeny of these rodents (Vucetich et al. 2005; Deschamps et al. 2007), an aspect that has been largely ignored so far because of the lack of appropriate samples.

Another caviomorph rodent documented for the Urumaco Formation includes an unidentified species of the dinomyid *Eumegamys* (Pascual and Díaz de Gamero 1969). Furthermore, faunal lists from Urumaco have included dental remains referred to *Tetrastylus*, *Telicomys* and Potamarchinae cf. *Potamarchus* and *Olenopsis* (Linares 2004). However, a revision of the referred specimens has not been done and most of these records are in need of verification (Horovitz et al. 2010). Geiger et al. (2013) distinguished four different morphotypes of giant caviomorphs from Urumaco based on an analysis of the femoral morphological variation and growth.

Neoepiblemids have been recorded in middle and late Miocene deposits of Brazil, Argentina and Peru (Horovitz et al. 2010; Tejada-Lara et al. 2015) (Fig. 1). An almost complete cranium and several mandibular remains of *Neoepiblema ambrosettianus* have been described for the late Miocene of Acre, Brazil (Bocquentin-Villanueva et al. 1990; Negri and Ferigolo 1999). Rodents are one of the most diverse groups registered in the Acre region with ten genera and twelve species, eleven of which are neoepiblemids and dinomyids (Ribeiro et al. 2013;

Table 1 Summary of dental traits, age and geographic distribution of the recognized members of *Phoberomys* and *Neoepiblema*

Taxon	Dental traits	Locality	Age	Reference
Phoberomys Kraglievich 1926	M3 with seven to eight laminae united labially, p4 with four laminae, the first two or three united labially and the third or fourth or just the fourth free			Bondesio and Bocquentin-Villanueva (1988)
Phoberomys insolita Kraglievich 1940	M3 with eight laminae united labially	Mesopotamia, Argentina	Late Miocene (Huayquerian)	Kraglievich 1940
Phoberomys pattersoni Mones 1980	M3 with seven laminae united labially. P4 with four laminae, the two anterior ones united labially, the posterior ones free	Urumaco, Venezuela	Late Miocene	Bondesio and Bocquentin-Villanueva (1988), Mones (1980)
Phoberomys lozanoi Kraglievich 1926	M3 with eight laminae united labially, the eighth one is poorly developed and not visible in oclusal view	Mesopotamia, Argentina	Late Miocene (Huayquerian)	Kraglievich (1940)
Phoberomys burmeisteri Kraglievich 1926	p4 with four laminae, the two anterior ones united labially and two posterior ones free	Mesopotamia, Argentina and Acre, Brazil	Late Miocene (Huayquerian)	Kraglievich (1926, 1932)
Phoberomys praecursor Kraglievich (1932	p4 with four laminae, the three anterior ones united labially and fourth one free	Mesopotamia, Argentina	Late Miocene (Huayquerian)	Kraglievich (1932)
Phoberomys bordasi Patterson 1942	p4 with four laminae, the three anterior ones united labially and the fourth free	Acre, Brazil	Late Miocene (Huayquerian)	Patterson (1942)
Phoberomys minima Kraglievich 1940	Lower molars smaller than *P. lozanoi* and larger than *Neoepiblema*	Mesopotamia, Argentina and Acre, Brazil	Late Miocene (Huayquerian)	Kraglievich (1940)
Neoepiblema Ameghino 1889	M3 with four laminae united labially, p4-m3 with three laminae, the first two united labially and the third free. In the p4 the third prism free or united lingually to the second			Negri and Ferigolo (1999)
Neoepiblema ambrossetianus Ameghino 1889	Molars larger than *N. horridula*. Second and third laminae of P4-M3 more transversal than *N. horridula*	Mesopotamia, Argentina and Acre, Brazil	Late Miocene (Huayquerian)	Negri and Ferigolo (1999), Bocquentin-Villanueva et al. (1990)
Neoepiblema horridula Ameghino 1889	As for the genus	Mesopotamia, Argentina and Acre, Brazil	Late Miocene (Huayquerian)	Ameghino (1889)

Kerber et al. 2015). The late Miocene sediments from the Paraná region, Argentina, include terrestrial mammals from the Ituzaingó Formation, which counts under its rodent fauna several members of the Neoepiblemidae (*Phoberomys* and *Neoepiblema*) (Cione et al. 2000; Nasif et al. 2013). Additional records of Neoepiblemidae include *Neoepiblema* sp. in Fitzcarrald, Peru (Tejada-Lara et al. 2015), and the San Gregorio Formation, Pliocene of Venezuela (Vucetich et al. 2010c).

In this work we describe new dental and cranial remains of giant rodents from the Urumaco Formation providing evidence of a higher rodent diversity and morphological disparity than previously recognized. We quantify the dental size variation in *Phoberomys* and *Neoepiblema*, and we show that the morphological variation in neoepiblemid rodents from Urumaco does not just represent intraspecific variation within *P. pattersoni*, the only species from this group previously described for the Urumaco fauna.

Materials and methods

We investigated the dentition of neoepiblemid specimens from Urumaco, Venezuela, and Mesopotamia, Argentina, as well as different taxa described in the literature. In order to have a clear view of the occlusal surface of the dentition, we sectioned the upper and lower dentition of ten specimens from Urumaco. We first stabilized the samples surrounding the teeth with the resin Technovit® 5071, and we cut the dentition with a sawblade along the anteroposterior axis, at about 50 mm from the occlusal surface. For each tooth available, we measured the anteroposterior length (AP), anterior width (AW), posterior width (PW) and medium width (MW). For the M3, as it has multiple laminae, we only measured the AP and PW. Measurements were taken with calipers to the nearest 0.1 mm. For the dental terminology we follow Negri and Ferigolo (1999) and Bondesio and Bocquentin-Villanueva (1988). Our use

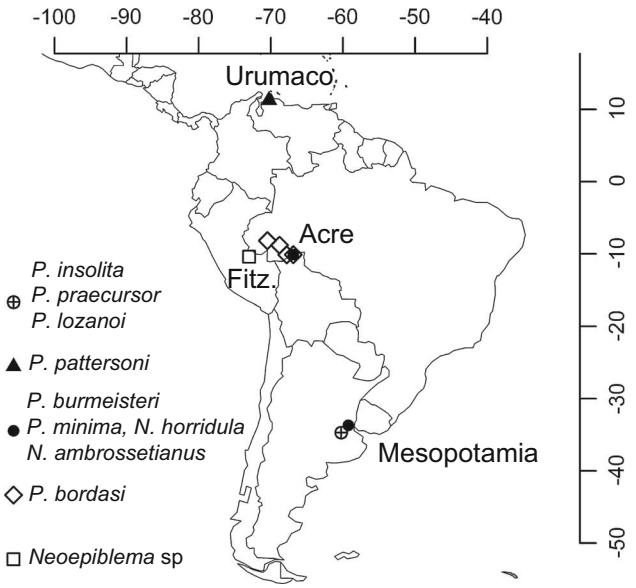

Fig. 1 Distribution of *Phoberomys* and *Neoepiblema* in South America. *Fitz* Fitzcarrald. Data downloaded from the Paleobiology database on 26 November 2014 using group names = *Phoberomys*, *Neoepiblema*, region = South America

of the term "laminae" is equivalent to "prisms" as used by Mones (1980).

For the quantitative analysis of the dentition, we performed a bivariate plot of the logarithm (log) of AW vs. log of AP. We grouped in the analysis the P4–M2 for the upper dentition and m1–m3 for the lower dentition because they are morphologically indistinguishable when dealing with isolated teeth. We did a linear regression for each set of teeth. The plots and regressions were made with R (R core team 2014).

Systematic paleontology

Rodentia Bowdich, 1821
Hystricognathi, Tullberg, 1899
Chinchilloidea Bennett, 1833
Neoepiblemidae, Kraglievich, 1926

Neoepiblema Ameghino, 1889
Neoepiblema sp.

Material AMU-CURS 381, partial left dentary with p4–m3.

Provenance NW San Rafael (11°14′52″N, 70°14′06″W), Urumaco Formation, upper member (Fig. 2).

Description AMU-CURS 381 has three laminae in the p4, the two anterior ones united labially and the third one free, as *Neoepiblema* (Negri and Ferigolo 1999). The mandibular symphysis extends posteriorly up to the middle anterior portion of p4, as described for *N. ambrosettianus* (Mones and Toledo 1989), but also true for *P. pattersoni* (AMU-CURS 53 and AMU-CURS 170, see below). AMU-CURS 381 have only three laminae in p4, in contrast with *Phoberomys* that has four, the first two connected labially (Bondesio and Bocquentin-Villanueva 1988). The m1–m3 of AMU-CURS 381 have three laminae, all of them free (Fig. 3a); in contrast to the other species of *Neoepiblema* that have three laminae in the lower molars, the second connected labially to the first and the third free (Negri and Ferigolo 1999). AMU-CURS 381 differs from some specimens referred to *Neoepiblema ambrosettianus* in having the third prism of the p4 free and not connected lingually to the second (Mones and Toledo 1989; Bocquentin-Villanueva et al. 1990).

We assigned AMU-CURS 381 to *Neoepiblema* based on the morphology and number of laminae of the p4. The fact that the m1–m3 of AMU-CURS 381 have three free laminae suggests that the labial connection between the first and second prism in m1–m3 is a variable character for *Neoepiblema*

Phoberomys Kraglievich, 1926
Phoberomys sp. A

Material AMU-CURS 382, partial left mandible with p4 only preserved at the alveolar level and m1–m3 poorly preserved. UNEFM-VF 014, with this catalog number, there are two partial mandibles, one right dentary with p4–m3, which we refer to *Phoberomys* sp. A, and a second right dentary with m1–m3 identified as *Phoberomys* sp.

Provenance AMU-CURS 382 comes from NW San Rafael (11°14′52″N, 70°14′06″W), Urumaco Formation, upper member (Fig. 2). UNEFM-VF 014 comes from Urumaco Formation, Urumaco.

Description AMU-CURS 382 and UNEFM-VF 014 exhibit features described for both *Phoberomys* and *Neoepiblema.* The p4 has four laminae, the two anterior ones connected labially and the third and fourth free, as in *P. pattersoni* and *P. burmeisteri* (Kraglievich 1926, 1932; Bondesio and Bocquentin-Villanueva 1988) (Fig. 3b). Due to its preservation it is difficult to observe the number and pattern of laminae in m1 and m2 for AMU-CURS 382; however, it is possible to state they are three, and they all seem to be free as in *Phoberomys*. In UNEFM-VF 014, the m1–m2 have three free laminae. The m3 has three laminae, the two anterior ones connected labially, as in *Neoepiblema* (Negri and Ferigolo 1999). The molar dimensions of these specimens are small compared to specimens referred to *P. pattersoni* (Table 2).

In contrast with AMU-CURS 382 and UNEF-VF 014, the p4 of *P. bordasi* and *P. praecursor* has the three anterior laminae united labially and the fourth free (Kraglievich 1932; Patterson 1942). These specimens differ

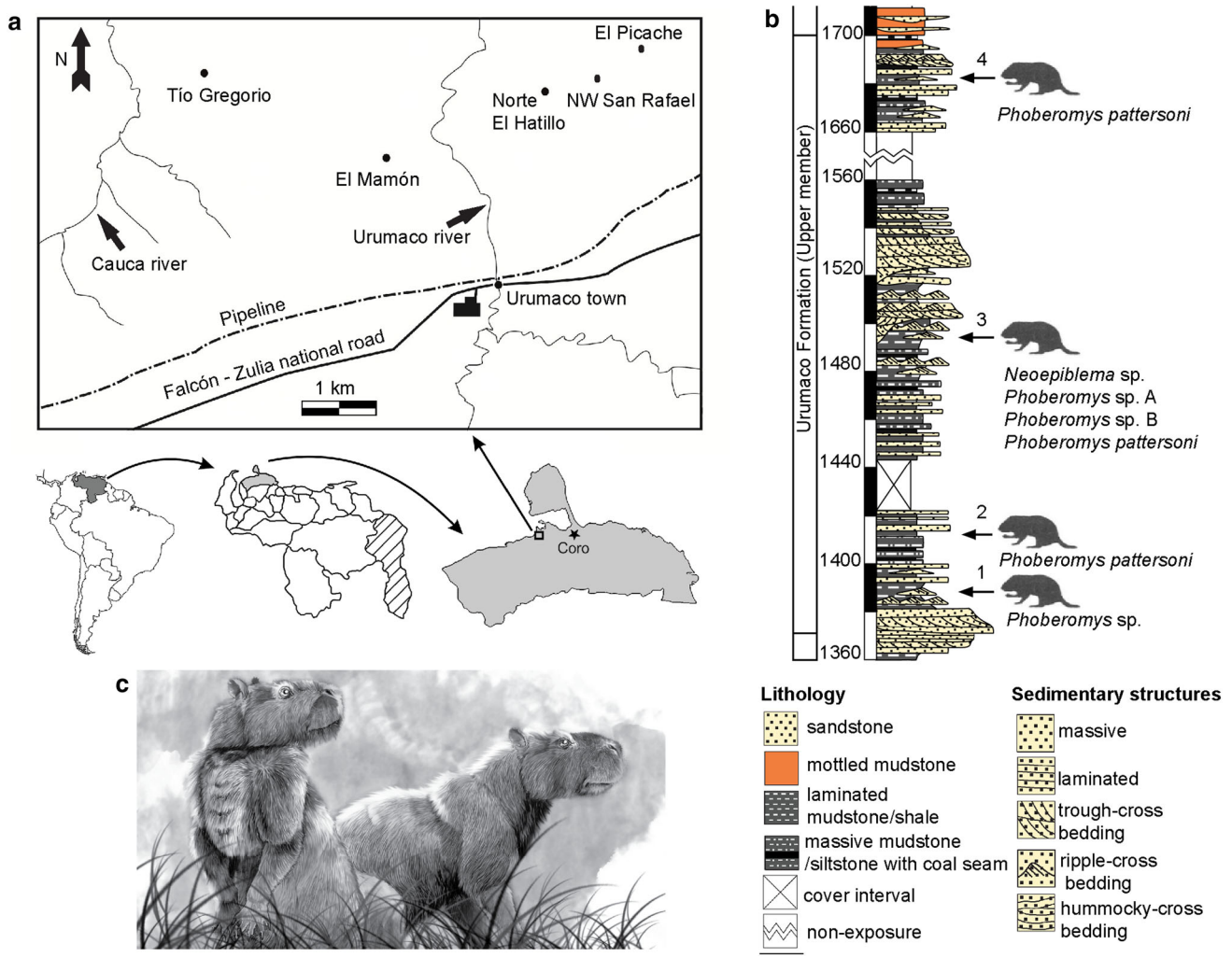

Fig. 2 Geographic and stratigraphic occurrence of neoepiblemids from Urumaco; **a** fossil localities and **b** stratigraphic profile of the upper member of the Urumaco Formation; the taxonomic occurrence of neoepiblemid taxa is indicated for each locality: (1) El Hatillo, (2) El Mamón, (3) El Picache/NW San Rafael and (4) Tío Gregorio/Cerro José La Paz. Modified from Quiroz and Jaramillo (2010) and Scheyer et al. (2013); **c** restoration of *P. pattersoni*. Artwork by Jorge González, modified from Horovitz et al. (2010)

from *Neoepiblema* in that the p4 of the latter has only three laminae (Negri and Ferigolo 1999). We therefore assigned AMU-CURS 382 and UNEFM–VF 014 to *Phoberomys* based on the morphology and laminae of the p4. The labial connection between the first and second laminae in m3 is a variable character in *Phoberomys* and neoepiblemids in general, as was mentioned above for AMU-CURS 381 referred to *Neoepiblema* sp.

Phoberomys sp. B

Material AMU-CURS 380—maxilla with right M1–M3 and left M3. AMU-CURS 35, partial maxilla with right P4–M3 and left P4–M1. MCN 66–72 V, isolated M3.

Provenance AMU-CURS 380 comes from NW San Rafael (11°14′52″N, 70°14′06″W), Urumaco Formation, upper member. AMU-CURS 35 comes from El Picache, Urumaco Formation, upper member (Fig. 2). MCN 66–72 V is from Urumaco Formation, Urumaco.

Description AMU-CURS 380 shows some diagenetic deformation, as the maxilla is slightly folded toward the left side. It preserves the right M1–M3 and the left M3. It is not possible to observe clearly the morphology of laminae in M1, but it has three laminae connected labially in M2. AMU-CURS 35 shows the P4–M2 with three laminae connected labially.

AMU-CURS 380, AMU-CURS 35 and MCN 66–72 V differ from other specimens of *Phoberomys* in the number of laminae of M3. The M3 of these specimens have six laminae (Fig. 3f, g), all connected labially, and it narrows posteriorly. In contrast, the M3 of other *Phoberomys* species have seven to eight laminae connected labially (Bondesio and Bocquentin-Villanueva 1988). The relative

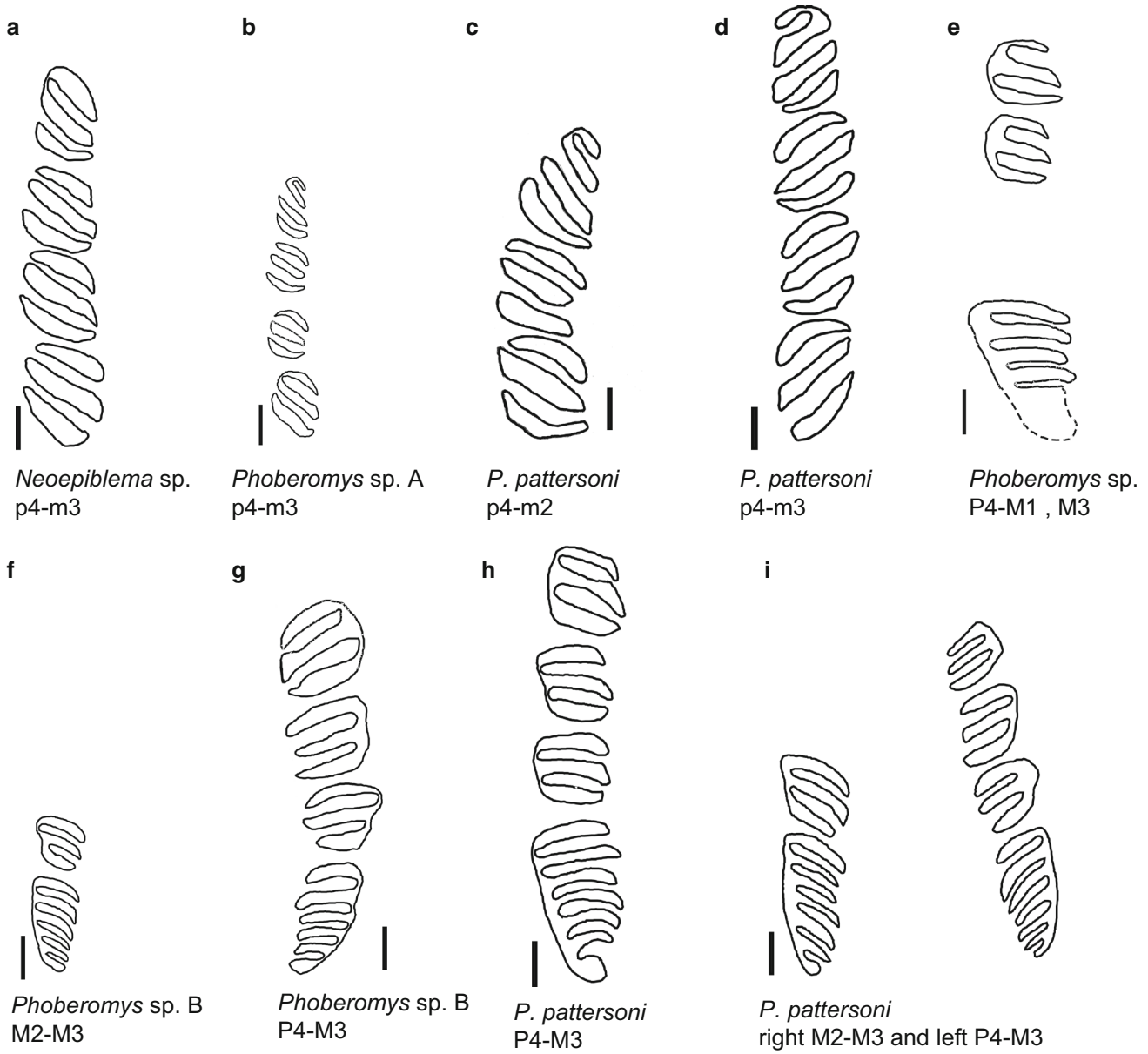

Fig. 3 Occlusal surface morphology of the neoepiblemids from Urumaco. **a** Lower dentition *Neopiblema* sp. (AMU-CURS 381); **b** lower dentition *Phoberomys* sp. A, (AMU-CURS 382); **c** lower dentition *P. pattersoni* (AMU-CURS 454); **d** lower dentition *P. pattersoni* (AMU-CURS 170); **e** upper dentition *Phoberomys* sp. (AMU-CURS 161); *dashed lines* represent the portion of M3 where the occlusal morphology could not be observed; **f** upper dentition *Phoberomys* sp. B (AMU-CURS 380); **g** upper dentition *Phoberomys* sp. B (AMU-CURS 35); **h** upper dentition *P. pattersoni* (AMU-CURS 255); **i** upper dentition *P. pattersoni* (AMU-CURS 53). *Scale bar* 10 mm

dimensions of the dentition of these specimens are small compared to other specimens referred to *Phoberomys* (Table 2).

Phoberomys sp.

Material AMU-CURS 161—complete cranium compressed in the dorsal-ventral plane.

Provenance AMU-CURS 161 comes from Norte El Hatillo, Urumaco Formation, upper member (Fig. 2).

Description AMU-CURS 161 is tentatively assigned to *Phoberomys* because it presents more than four laminae connected labially in the M3, although is not possible to assess the total number of laminae because of the preservation of the posterior portion of the M3. *Phoberomys* has 7–8 laminae in M3 (Bondesio and Bocquentin-Villanueva 1988); in contrast *Neoepiblema* have only four laminae (Negri and Ferigolo 1999). The P4–M1 of AMU-CURS 161 have three laminae connected labially as in all

Table 2 Dental measurements of neoepiblemids

Taxon	Catalog number	Tooth	Left				Right			
			Length	Width			Length	Width		
			AP	AW	PW	MW	AP	AW	PW	MW
Phoberomys sp.	AMU-CURS 161	P4					15.6	12.9	16.1	15.7
		M1					18.2	17.2	14.8	15
		M2					17.5	19.6	16.4	?
		M3					27.3	20.7	11.4	NA
	UNEFM TG4	P4					28.6	28.5	22.1	?
		M1					21.1	21.6	20.6	21
		M2					19.3	23.5	20.3	22.2
		M3					41.1	22	13.1	NA
	UNEFM 1438	M1	17.7	16.2	13.7	15				
		M2	19.3	17	14.1	18				
	MACN-Pv 2645	p4					11.6	7.4	7.6	8.3
	UNEFM-VF 014	m1					20.7	14.8	14.7	16.7
		m2					22.6	16.8	19.3	17.6
		m3					26.2	18.3	17.6	21.8
	MACN-Pv 3475	m1–m3					25.4	20.6	20.9	23.7
	CIAAP 1438[b]	M1	16.9	17						
		M2	18.3	18.3						
		m2					22.6	16.5		
Phoberomys sp. A	AMU-CURS 382	p4	17	?	12.8	?				
		m1	15.2	9.9	11.7	?				
		m2	15.9	8.6	10.7	10.8				
		m3	19.7	10.4	10.5	9.6				
	UNEFM-VF 014	p4					15	14.8	10.9	11.9
		m1					14	11.7	12	12.2
		m2					15.4	12.2	11.7	13.5
		m3					15.3	11.5	11.8	13.2
Phoberomys sp. B	AMU-CURS 380	M1	15.4	13	9.9	?				
		M2	13	12.8	8.3	11.7				
		M3	23.1	12.2	5.5	NA				
	AMU-CURS 35	P4	24.1	13.9	18.1	14.1				
		M1	20.5	17.2	15.4	17				
		M2	16.6	16.9	?	?				
		M3	28.2	13.5	7.6	NA				
	MCNC 66–72 V	M3	15.1	9.1	6.7	NA				
P. insolita	MACN-Pv 13480	P4–M2	17	20.2	20.3	21.4				
	MACN-Pv 4068	P4–M2	21.5	22.2	19.6	21.8				
	MACN-Pv 3290	P4–M2					22.2	21.9	22	22.7
P. pattersoni	AMU-CURS 255	P4	21.3	13.5	12.8	?	21.4	11	11	?
		M1	19.2	16.6	14.8	?	18.6	13.2	14.4	?
		M2	17	16.2	14.1	?	18.5	15.5	15	?
		M3	33.5	14.3	6.4	NA	36.6	20.4	9.9	NA
	MCNC 12-72 V	M3	33.6	17.1	7.1	NA				
	AMU-CURS 39	P4	25.2	22.4	24.6	22.5	26.5	19.8	22.7	22.7
		M1	26.5	21	22.3	24.4	19.9	19.5	20.3	22.4
		M2	22.2	20	21	23.6	19.6	22.5	19.1	20.8
		M3	48	22.4	20.4	NA	49.3	22.4	13.3	NA
		p4					32.7	14.2	21.1	21.4
		m1					?	?	?	23.4
		m2					26	25.2	22.6	?
		m3					29.3	26.8	27.4	26.2

Table 2 continued

Taxon	Catalog number	Tooth	Left				Right			
			Length	Width			Length	Width		
			AP	AW	PW	MW	AP	AW	PW	MW
	AMU-CURS 53	P4	26.1	15.1	17.3	?	?	?	17.6	?
		M1	22.9	?	15.5	?	21.8	17.6	16	?
		M2	22	18.8	14	17.1	21.8	17.7	12.5	17
		M3	38.5	15	10.5	NA	42.3	18.4	9	NA
		p4	26.4	14.6	15.2	?				
		m1	25.9	14.9	13	?				
		m2	25.6	15.2	13.6	?				
		m3	26.4	15.5	11.4	?				
	AMU-CURS 454	p4	31.9	12.6	28.3	13.4				
		m1	23.5	18.2	20.4	21.4				
		m2	25.5	19.4	23.9	22.2				
		m3	27.5	24.1	17.5	?				
	AMU-CURS 170	p4					25.5	11.6	14.7	15.3
		m1					23.7	15.2	18.5	18.8
		m2					24.3	15.2	18.5	18.8
		m3					27.6	17.8	14.4	16.5
	MCNC 104–72 V	m3	36.9	22.4	22	26.6				
	UNEFM-VF 020[b]	P4					27.9	20.8		
		M1					20.6	21		
		M2					18.6	21		
		M3					41	20.7		
P. praecursor	MACN-Pv 9026	p4	28.7	11.8	22.2	19.4				
P. burmeisteri	MACN-A 5831 (Type)	P4–M2	21	23.8	26	31.4				
	MLP 15-254	p4					33.3	24.2	22.5	22.3
	MLP 15-257	p4					32.8	21.1	24.5	22
	MACN-Pv 4729	p4					30.8	12.8	19.5	20.2
	MLP 12-246	m1	23.8	20.3	21	20.5				
		m2	25.3	20.8	21.6	21.8				
		m3	32	22.2	23	21.2				
	MACN-Pv 2494	m3					36.8	24.4	28	28.8
	MACN-Pv 6620	m1–m3	28.6	20.5	22.5	20.4				
	MACN-Pv 3288	m1–m3					26.6	20.2	24	23.7
P. lozanoi	MLP 36[c]	M3	34	14.5	8.5	NA				
P. bordasi	AMNH 22666[f]	p4					16.4	4	13.3	13.7
		m1					16.5	12	14.5	15.7
P. minima	MACN-Pv 3461	P4–M2	13.7	12.8	12.7	15.7				
Neoepiblema sp.	MLP 73-I-10-2	P4–M2					11.7	9	10.5	9.9
	AMU-CURS 381	p4	22	15	14	14.6				
		m1	18.8	14.7	16.6	14.5				
		m2	18.3	17	18.6	19				
		m3	23.5	18.5	17	19.7				
	MLP 15-420a	m1–m3	10.3	5.8	7.7	8.3				
	MLP 15-419a	m1–m3	10.5	7.7	8.9	8.6				
	MLP 15-421	m1–m3	12.4	8.5	11.6	9.7				
	MLP 41-XII-13-4102	m1–m3					13.4	11.7	11.7	11.6

Table 2 continued

Taxon	Catalog number	Tooth	Left				Right			
			Length	Width			Length	Width		
			AP	AW	PW	MW	AP	AW	PW	MW
N. horridula	MACN-Pv 2609	P4					12.4	8.5	8.7	10.2
		M1					11.8	9.2	8	9.8
		M2					11.9	9.2	7.8	9.8
		M3					15.7	9	4.6	NA
	MLP 69-XII-2-20 (Type)	M3					12.6	5.6	7.2	NA
	MACN-Pv 13414	M3	14.9	8.8	5.9	NA				
	MACN-Pv 15318	M3					10	5.9	3.4	NA
	MLP 73-I-10-4	P4–M2					7.1	4	4.8	4.7
	MACN-Pv 13365	P4–M2	10.5	8	7.6	8.4				
	MACN-Pv 13362	P4–M2					10	7.9	9.4	10.2
	MACN-Pv 9036	P4–M2	11.6	8.9	7.4	8.6				
	MACN-Pv 4504	P4–M2	9.8	8.6	7.3	8.8				
	MACN A 5874	P4–M2	8	7.7	7.4	7.7				
	MACN-Pv 3458	P4–M2	11.5	8.5	7.9	8.6				
		M3	15.6	8.8	6.4	NA				
N. ambrossetianus	MACN-Pv 4575	P4–M2					12.4	13.7	20	17.3
	MACN-Pv 4580	m1					8.3	4.5	6.2	5.9
		m2					7.8	5.4	6.4	6.5
	MACN-Pv 13473 (Type)	m1	13.5	7.7	10.4	10				
		m2	15.1	8.3	11.4	11.6				
	MACN-Pv 4576	m1–m3					14.7	14.1	17.6	16
	MACN-Pv 4542	m1–m3					11	8.1	9.7	8.1
	MACN-Pv 4031	m1–m3					11.1	7.7	8.4	11.4
	MACN-Pv 8885	m1–m3	13.7	9.5	11.1	11.5				
	MACN-Pv 3404	m1–m3					12.1	9.2	11.4	11.2
	MACN-A 5829	m1–m3	8.8	6.4	7.3	7.2				
	MACN-A 5830	m1–m3	8.4	6.9	9.8	9.2				
	MACN-Pv 2484	m1–m3	11.3	7.4	8.9	8.6				
	MACN-Pv 4480	m1–m3					6	4	4.5	5
	MACN-Pv 3276	m1–m3	11.3	7.2	8.4	8.8				
	MPEG PV-82[d]	p4	15	9	10	12				
		m1	15.5		13					
		m2	15.1		12					
		m3	15.3	8	13					
	UFAC 4515[e]	P4	16	11.7	12	15	16	11.8	12	15.2
		M1	15	12.8	14.4	11	15	13.1	11.5	14.7
		M2	15	13.1	12	14.6	15	12.8	12	14.2
		M3	22.2	12.2	10.2	NA	22	11.5	10.4	NA
	UFAC 1716[a]	M2					14	10.5		
		M3					21	10		
		p4	13.5	10						
		m1	12.5	11						
		m2	13	17						
		m3	10	11						
	UFAC 1490[a]	p4					16	9		
		m1					13.5	10		
		m2					13.5	10		
		m3					15.5	11		

Table 2 continued

Taxon	Catalog number	Tooth	Left				Right			
			Length	Width			Length	Width		
			AP	AW	PW	MW	AP	AW	PW	MW
	UFAC 1658[a]	p4	17	11						
	UFAC 1810[a]	p4					16	11.5		
		m1					16	13.5		
		m2					16	12		
		m3					19	11		

AP anterior-posterior length, *AW* anterior width, *PW* posterior width, *MW* medium width, *NA* not applicable

[a] Bocquentin-Villanueva et al. (1990)

[b] Horovitz et al. (2006)

[c] Kraglievich (1940)

[d] Mones and Toledo (1989)

[e] Negri and Ferigolo (1999)

[f] Patterson (1942)

neoepiblemids (Fig. 3e). The preservation prevents observing the morphology of laminae in M2. AMU-CURS 161 presents a strong diagenetic compression in the dorso-ventral plane and its bad preservation prevents observing most of the cranial sutures. The skull is long and narrow, with conspicuous sagittal and nuchal crests (Fig. 4). AMU-CURS 161 shares some traits with *Neoepiblema* such as the ventral root of the zygomatic process at the level of P4, and palatines present at the level of the middle portion of M3; these traits were included in the generic diagnosis of *Neoepiblema* by Negri and Ferigolo (1999), but they are also present in *P. pattersoni* (e.g., AMU-CURS 255, see below).

AMU-CURS 161 shares some traits with *N. ambrosettianus,* including: premaxilar elongated forming more than half of the diastema and a prominent sagittal crest projecting over the other elements of the cranium (Negri and Ferigolo 1999). The presence of a sagittal crest in a specimen originally referred to *P. pattersoni* by Bondesio, and Bocquentin-Villanueva (1988) (CIAAP 1438) was also mentioned by Horovitz et al. (2006), who referred the specimen to cf. *Phoberomys* while highlighting several differences between CIAAP 1438 and other specimens of *P. pattersoni*.

Phoberomys pattersoni, Mones 1980

Material AMU-CURS 255, complete cranium compressed in the dorsal-ventral plane and the anterior portion of the rostrum folded toward the lateral right plane. AMU-CURS 53, maxilla with right and left P4–M3 and partial left dentary with p4–m3. AMU-CURS 454, partial left mandible ramus with p4–m3, poorly preserved. AMU-CURS 170, a complete mandible with right and left p4–m3.

Provenance AMU-CURS 255 comes from El Picache, Urumaco Formation, upper member; AMU-CURS 39 and AMU-CURS 53 are from El Mamón, Urumaco Formation, upper member; AMU-CURS 454 comes from Cerro Jose La Paz (11°14′40″N, 70°09′44.3″W), Urumaco Formation, upper member and AMU-CURS 170 comes from Tío Gregorio, Urumaco Formation, upper member (Fig. 2).

Description AMU-CURS 255 is assigned to *P. pattersoni* based on the M3 with seven laminae connected labially (Fig. 3g) (Mones 1980; Bondesio and Bocquentin-Villanueva 1988) and the narrowing of the posterior portion of M3 at the level of the last three laminae (Mones 1980; Sánchez-Villagra et al. 2003). The P4–M2 have three laminae connected labially. The third lamina of P4 is concave anteriorly and has a "V" shape inflexion in its inner portion (Bondesio and Bocquentin-Villanueva 1988) (Fig. 3g). AMU-CURS 255 also presents a strong diagenetic distortion; it is compressed in the dorso-ventral plane, and the most anterior portion of the rostrum is folded toward the right lateral side (Fig. 4). Due to the preservation it is not possible to observe the cranial sutures. The skull does not show a well-developed sagittal crest as has been mentioned before for *P. pattersoni* (Sánchez-Villagra et al. 2003) and in contrast to *N. ambrossetianus* (Negri and Ferigolo 1999) and cf. *Phoberomys* (Horovitz et al. 2006). It is possible that the degree of development of the sagittal crest is related to age. AMU-CURS 255 has the anterior root of the zygomatic arch at the level of P4 as in *N. ambrossetianus* (Negri and Ferigolo 1999) and cf. *Phoberomys* (Horovitz et al. 2006).

AMU-CURS 53 is also assigned to *P. pattersoni* based on the number of laminae and morphology of the M3 (Fig. 3i). The P4–M2 have three laminae all connected

labially, as in all neoepiblemids. Although the specimen consists of a complete lower left dentition, the preservation of the specimen prevents the examination of diagnostic features of *P. pattersoni* in the p4. The m1–m3 have three laminae, apparently all free. AMU-CURS 454 and AMU-CURS 170 are identified as *P. pattersoni* based on the p4 morphology with four laminae, the two anterior ones connected labially and m1–m3 with three laminae, all free (Fig. 3c, d) (Bondesio and Bocquentin-Villanueva 1988). In AMU-CURS 53 and AMU-CURS 170, the mandibular symphysis extends posteriorly, reaching the anterior portion of the p4.

Quantitative analysis

The relationship between the anteroposterior length (AP) and anterior width (AW) of the upper and lower dentition in *Phoberomys* and *Neoepiblema* is different in the two genera, with *Neoepiblema* having a lower length to width ratio than *Phoberomys*, although the two taxa are within the same trajectory (Fig. 5a–d). For *Neoepiblema* we found that *N. horridula* is smaller than *N. ambrossetianus* and the dental morphospace of the two species does not overlap (Fig. 5a, b). Within *Phoberomys*, there is no clear differentiation of the dental morphospace among species (Fig. 5a–d).

For the M3 (Fig. 5a), there are two specimens assigned to *Phoberomys* sp. B (MCN 66–72 V and AMU-CURS 380), which overlaps with *Neoepiblema*; besides its small size, these specimens have six laminae in the M3. For the P4–M2 (Fig. 5b) and lower dentition (Fig. 5c, d), there is also a small overlap between the two genera. However, the overall pattern is the same, with *Neoepiblema* being smaller than *Phoberomys* and both genera falling within the same trajectory.

Discussion

Most of the neoepiblemid species currently recognized as valid are known from isolated or fragmentary upper or lower dentitions (for a summary of the systematic history of Neoepiblemidae, see Bondesio and Bocquentin-Villanueva, 1988: 32–33 and Negri and Ferigolo, 1999: 8–12). The most important characteristics considered for species definition within the group have been the number and morphology of laminae in premolars and molars and the relative molar size (e.g., Kraglievich 1940; Mones 1980; Patterson 1942). However, rodents with euhypsodont teeth have a wide range of ontogenetic and intraspecific morphological variation (Vucetich et al. 2005), which calls for caution for the definition of new taxa based on fragmentary material without an appropriate sample size. We found for example that the pattern of labial connections among the laminae in m1–m3 is a variable character in *Phoberomys* and *Neoepiblema* and should not be used as a characteristic to differentiate the two genera.

Until now, *P. pattersoni* and *Eumegamys* were the only big rodent taxa formally reported for the Urumaco Formation. We found evidence to support the recognition of a higher diversity of giant rodents from Urumaco and report for the first time the presence of *Neoepiblema* in this Formation. Vucetich et al. (2010c) reported *Neoepiblema* sp. for the San Gregorio Formation (late Pliocene) toward the top of the Urumaco sequence from an assemblage that also includes hydrochoerids and an octodontoid. The record of *Neoepiblema* in the Urumaco Formation confirms the presence of this taxon in the northern Neotropics since the late Miocene. The oldest record of *Neoepiblema* comes from the middle Miocene Fitzcarrald fauna (Tejada-Lara et al. 2015). Until now, no rodents from the Socorro Formation (middle Miocene) in the Uumaco sequence had been reported. In an expedition in January 2015, one of us (MRS-V) found a distal femur (AMU-CURS 641) of a giant rodent from the Socorro Formation. It is from East of Capirote (11°11′32.9″N, 70°11′22.4″W), the road to Quebrada Honda, the same locality reported by Head et al. (2006: 234) for snakes.

Previous work in the late Miocene deposits of Acre, in southern Brazil and Paraná, and in northern Argentina shows a high diversity of rodents. Given the postulated similarity of the Urumaco mammal assemblage with the Acre and, to a lesser extent, the Paraná assemblages (Cozzuol 2006; Carrillo et al. 2015), a higher diversity than recognized until now for Urumaco was only expected. This conclusion is supported by the previous study of morphological diversity in postcranial remains (Geiger et al. 2013).

The length-width relationship in the dentition shows a differentiation between the two neoepiblemid genera, with *Neoepiblema* having a lower length-to-width ratio than *Phoberomys.* Within *Neoepiblema, N. horridula* is smaller than *N. ambrossetianus*, and there is no overlap between the two species. In the case of *Phoberomys*, there is not a clear differentiation among the different species recognized within the genus, and they overlap along the trajectory of the dental morphospace, suggesting that some of these species could represent different ontogenetic stages of one or few taxa within *Phoberomys,* as has also been proposed for hydrochoerids (Vucetich et al. 2005; Deschamps et al. 2013). The possibility that the number of neoepiblemid species is lower than currently recognized has also been raised by other authors (Vucetich et al. 2010c; Nasif et al. 2013).

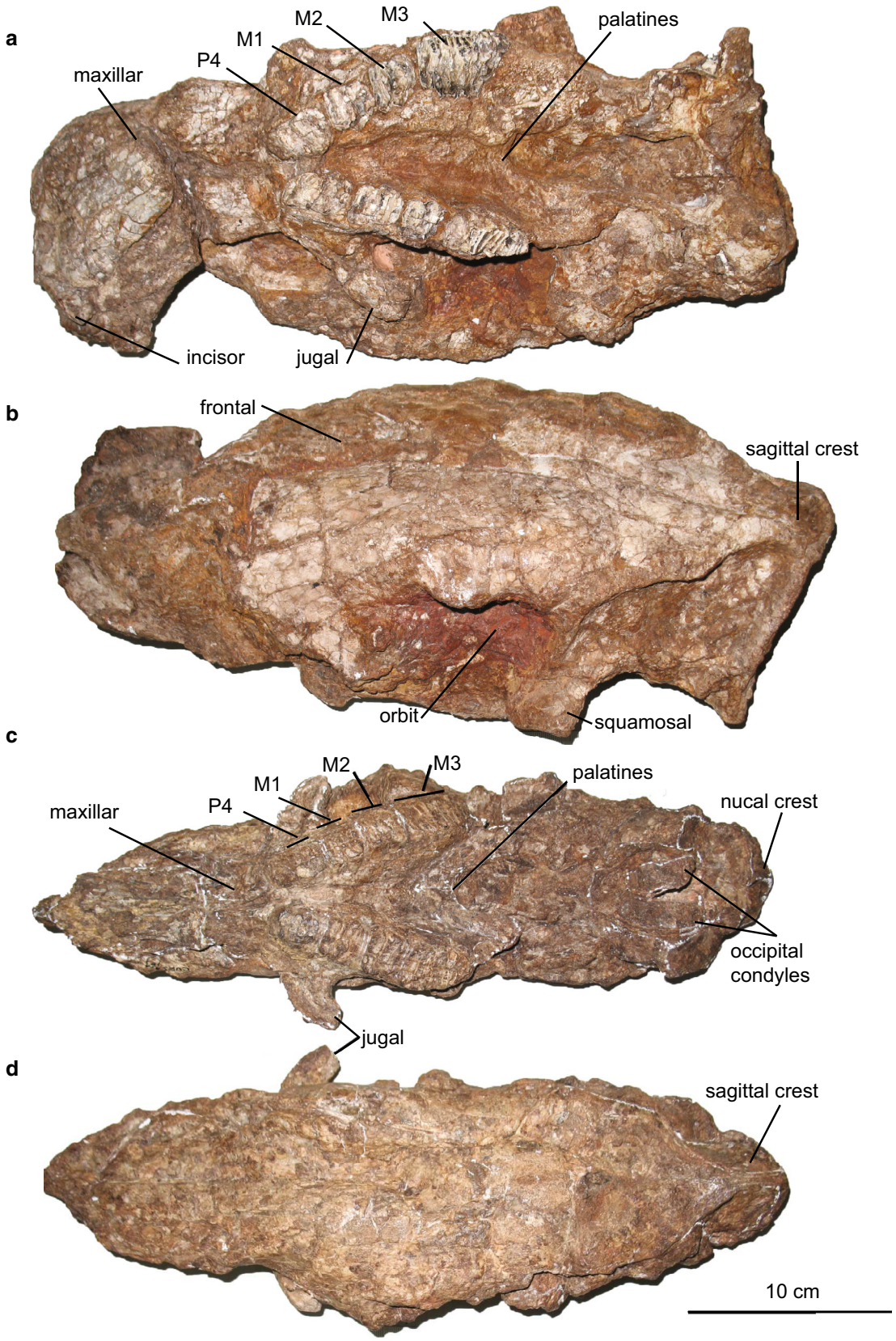

Fig. 4 Neoepiblemid skulls from Urumaco. *P. pattersoni* (AMU-CURS 255) **a** ventral view; **b** dorsal view. *Phoberomys* sp. (AMU-CUS 161) **c** ventral view; **d** dorsal view

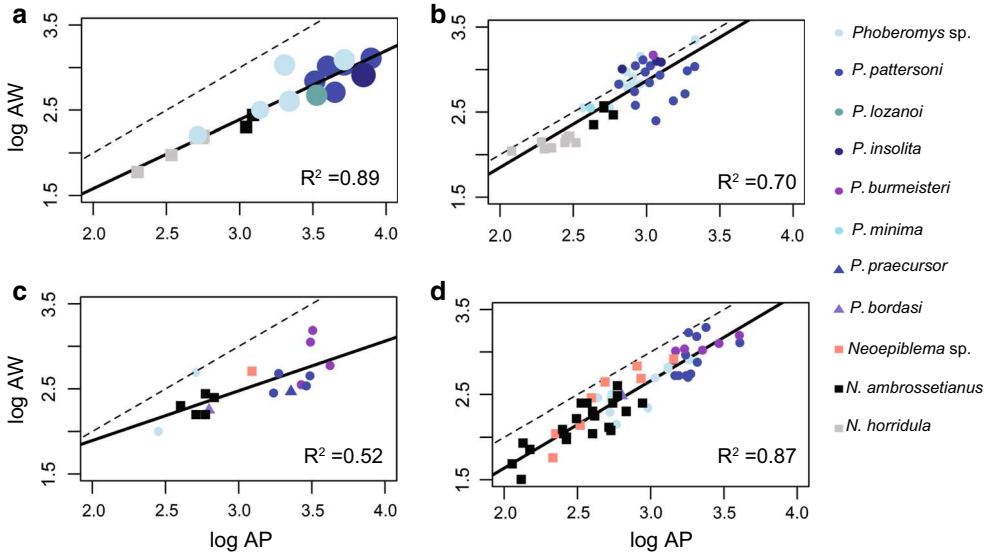

Fig. 5 Length-width relationship of the upper and lower dentition in Neoepiblemidae. **a** M3, the dot size is proportional to the number of laminae. **b** P4-M2. **c** p4, the dot size is proportional to the number of laminae. **d** m1-m3; *log AW* logarithm of anterior width, *log AP* logarithm of anterposterior length. *Solid line* regression line for log AW vs. log AP, R^2 value indicated in each panel; *dashed line* isometric line

In the upper dentition the M3 has been used to differentiate the different species of neoepiblemids (Table 1). The case of three small specimens referred to *Phoberomys* sp. B (AMU-CURS 380, AMU-CURS 35 and MCN 66–72 V) is interesting because they have six laminae on M3. The number of laminae on the M3 for *Phoberomys* ranges between seven and eight (Bondesio and Bocquentin-Villanueva 1988), and *Neoepiblema* has four laminae (Negri and Ferigolo 1999). We interpret the existence of six laminae in the M3 of small specimens assigned to *Phoberomys* as an indication of either the possibility of addition of at least one laminae in the M3 during growth or as a higher variability in this area of dental anatomy than currently recognized.

Conclusion

A higher diversity of giant rodents in the Urumaco Formation is reported with the finding of *Neoepiblema* sp. There have been questions about the validity of the several neoepiblemid species currently recognized. Our dental and quantitative analysis of Neoepiblemidae shows a differentiation between *Phoberomys* and *Neoepiblema*, although both genera fall within the same trajectory. Within *Neoepiblema*, *N. horridula* is smaller than *N. ambrossetianus*; the differentiation on size between the two species of *Neoepiblema* suggest that they are both valid taxa. In contrast, in *Phoberomys* there is not a clear differentiation among the different species recognized for the genus, suggesting that some could represent different ontogenetic stages of one or a few taxa.

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